

# Simulating the impacts of climate change on soybean cyst nematode and the distribution of soybean

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## ABSTRACT

Climate change will undoubtedly impact air and soil temperature in the future. For agriculture, climate warming could be beneficial by opening new lands to profitable crops at higher latitudes. In Canada, soybean production has had a spectacular growth over the last five years with an increase of 27% in the acreage devoted to its cultivation. However, the anticipated climatic changes, coupled with global trading intensification could also favor the introduction and establishment of invasive alien soybean pests. For example, the soybean cyst nematode (SCN) has recently been discovered in the province of Québec, Canada and its presence raised several questions on its reproductive potential, spatial distribution and possible impacts on long term soybean cultivation. To investigate the consequences of climate warming on soybean and SCN development and distribution, and their interactions, two phenology models have been developed and used with the Representative Concentration Pathways (RCP) 4.5 and 8.5, associated with climate change scenarios. These pathways describe two possible future climates based on the level of greenhouse gases concentration in air. Using temperature optimum for soybean maturity group I, our results showed that soybean could be cultivated over all cropland of Québec by the 2050 horizon (2041–2070). Based on phenology models, SCN can currently complete from one to three generations in the different regions of Québec. In the future, the nematode could produce up to four or five generations in an optimistic (RCP 4.5) or pessimistic (RCP 8.5) scenario, respectively. Climate warming will promote the expansion of soybean production to northern areas and expected conditions will be more favourable to SCN development. Accordingly, we should develop more soybean lines with an early maturity and containing other sources of resistance than PI88788 to reduce its reproduction capacity under a more favourable climate in the future.

## 1. Introduction

In an era of major changes, the sustainability of food production is under threat (Sundström et al., 2014; Food and Agriculture Organization of the United Nations (FAO), 2017). Although trade globalization has been beneficial on several aspects, the introduction of many invasive alien species (IAS), has altered agricultural ecosystems and caused losses to the economy (FAO, 2017). In addition, even if empirical evidence is still limited, numerous model studies have predicted that the increasing temperature and atmospheric CO<sub>2</sub> concentration accompanying climate change will have a high impact on agriculture (Savary et al., 2012; Sundström et al., 2014; Bhattarai et al., 2017; Zhao et al., 2017; Deutsch et al., 2018). Based on Representative Concentration Pathways (RCP), which describe greenhouse gas

concentration trajectories, the latest report on climate change by the Intergovernmental Panel on Climate Change [Interpanel on Climate Change \(IPCC\) \(2014\)](#) projects a rise in global mean temperature of 0.3 to 4.8 °C and in CO<sub>2</sub> atmospheric concentration from about 420 ppm to 935 ppm by the late-21st century.

The worldwide production of basic food commodities largely depends on 15 crops (Strange and Scott, 2005), including soybean (*Glycine max* L. Merr.), which ranks sixth in production and fourth in cultivated area (FAOSTAT, 2017a,b). Soybean ranks high in protein and other essential nutrients and plays a major role in meeting global food security objectives (Strange and Scott, 2005; Savary et al., 2012). One of the main pathogens of soybean is the soybean cyst nematode (SCN) (*Heterodera glycines* Ichinohe), a below-ground obligate endoparasite that has been accidentally introduced in North America from Asia

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(Wrather et al., 2010). In the USA, this species causes over \$1 billion in annual losses in most soybean-producing counties where it has been introduced and become an IAS (Wrather and Koenning, (2009); Wrather et al. (2010). Since its first detection in 1954 in North Carolina, SCN has quickly spread across North America via biotic (humans, animals) and abiotic (wind, water) vectors (Riggs, 2004; Tylka and Marett, 2014). In Canada, SCN was first detected in 1987 in Kent County, Ontario (Anderson and Welacky, 1988; Riggs, 2004) and in Québec in 2013 (Mimee et al., 2014). This recent invasion provides a unique opportunity to study the biology of SCN during its phase of establishment. At northern latitudes, the potential is high for expansion of soybean production, as well as for naturalization and spread of SCN (Bootsma et al., 2005; Osborne et al., 2012).

Climate change will impact the interaction between soybean and SCN. For instance, climate warming will favour the expansion of cultivated areas for soybean by increasing the length of the growing season which, in return, could open new establishment areas for SCN as seen for others species like the brown marmorated stink bug which is actually spreading in eastern Canada (Bootsma et al., 2005; Bebbler et al., 2013; Kistner, 2017). Furthermore, environmental changes caused by climate warming can influence the capacity of plants to cope with biotic stresses, possibly increasing their susceptibility to parasitic infections (Anderson et al., 2004; Grulke, 2011; Newton et al., 2012). As for all poikilotherm organisms, high temperature reduces the developmental time of SCN (Lauritis et al., 1983; Bonner and Schmitt, 1985) thereby potentially increasing the number of generations per growing season and result in increased damage to soybean production.

Climate change will modify local environmental conditions in most cropping systems but the impacts on host-parasite interactions and yield remain unknown (Donnatelli et al., 2017). The soybean – nematode relationship could represent a good model to study the impact of climate change on a below-ground endoparasite establishment capacities, reproduction and time of infection in function of rising soil temperature. In this study, we use bioclimatic models to predict the impacts of climate warming on soybean and SCN phenology in Québec, by comparing a reference climate period (1981–2010) to two climatic scenarios, RCP 4.5 and RCP 8.5, of CO<sub>2</sub> concentrations associated with the 2041–2070 period (referred to as 2050 horizon) (Interpanel on Climate Change (IPCC) (2014). Furthermore, a case study is presented to illustrate direct impacts of climate warming during a growing season at field scale. We also propose the use of geographic information systems (GIS) to visualize the effects of climate change on expected (i) soybean growing area, (ii) SCN establishment area, and (iii) SCN reproductive capacity and seasonal population dynamics.

## 2. Material and methods

### 2.1. Study area

The study area included all agricultural land in Québec as determined by Agriculture and Agri-Food Canada, AAFC (2015). (Fig. 1). We used the Québec Lambert projection for all maps and the North American Datum of 1983 (NAD83) as the geodesic reference.

### 2.2. Climate data of recent years (1981–2010) and climate scenarios of the future (2041–2070)

The air temperatures for the reference years (1981–2010) were selected from the *Daily 10 km Raster-Gridded Climate Dataset for Canada 1950–2012* available on the website of AAFC's National Land and Water Information Service (NLWIS). This dataset includes daily maximum and minimum air temperatures, and precipitations recorded from 1950 to 2012 and interpolated with ANUSPLIN 4.3 software (Hutchinson, 2004) on a 10 km X 10 km grid (Hutchinson et al., 2009) covering approximately 7500 weather stations across Canada.

The future simulations and projections for 2050 horizon

(2041–2070) are based on two CO<sub>2</sub> RCPs developed by IPCC (2014). For projections, we selected an intermediate CO<sub>2</sub> emission pathway (RCP 4.5) and a pessimistic CO<sub>2</sub> emission pathway (RCP 8.5) to foresee the effects of temperature variations on the seasonal phenology of soybean and SCN. Under the intermediate projection (RCP 4.5), global mean surface temperatures are projected to increase from 1.1 °C to 2.6 °C until the end of the century (2100) accompanied by an average atmospheric CO<sub>2</sub> concentrations from 580 ppm to 720 ppm (≈ 650 ppm CO<sub>2</sub>) (Van Vuuren et al., 2011). Under the most pessimistic projection (RCP 8.5), global mean surface temperatures are projected to increase from 2.6 °C to 4.°C accompanied by an average atmospheric CO<sub>2</sub> concentration near 1390 ppm CO<sub>2</sub> (Van Vuuren et al., 2011).

Ten global climate models from the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Table 1) were used for each RCP CO<sub>2</sub> emission trajectories to simulate the projected climate for the 2050 horizon CMIP5 (2015).

A total of 20 simulations were performed, 10 for each of the two CO<sub>2</sub> RCPs. The temperature forecasts associated with both RCP emission pathways are based on the average of the data obtained from these simulations (Table 1).

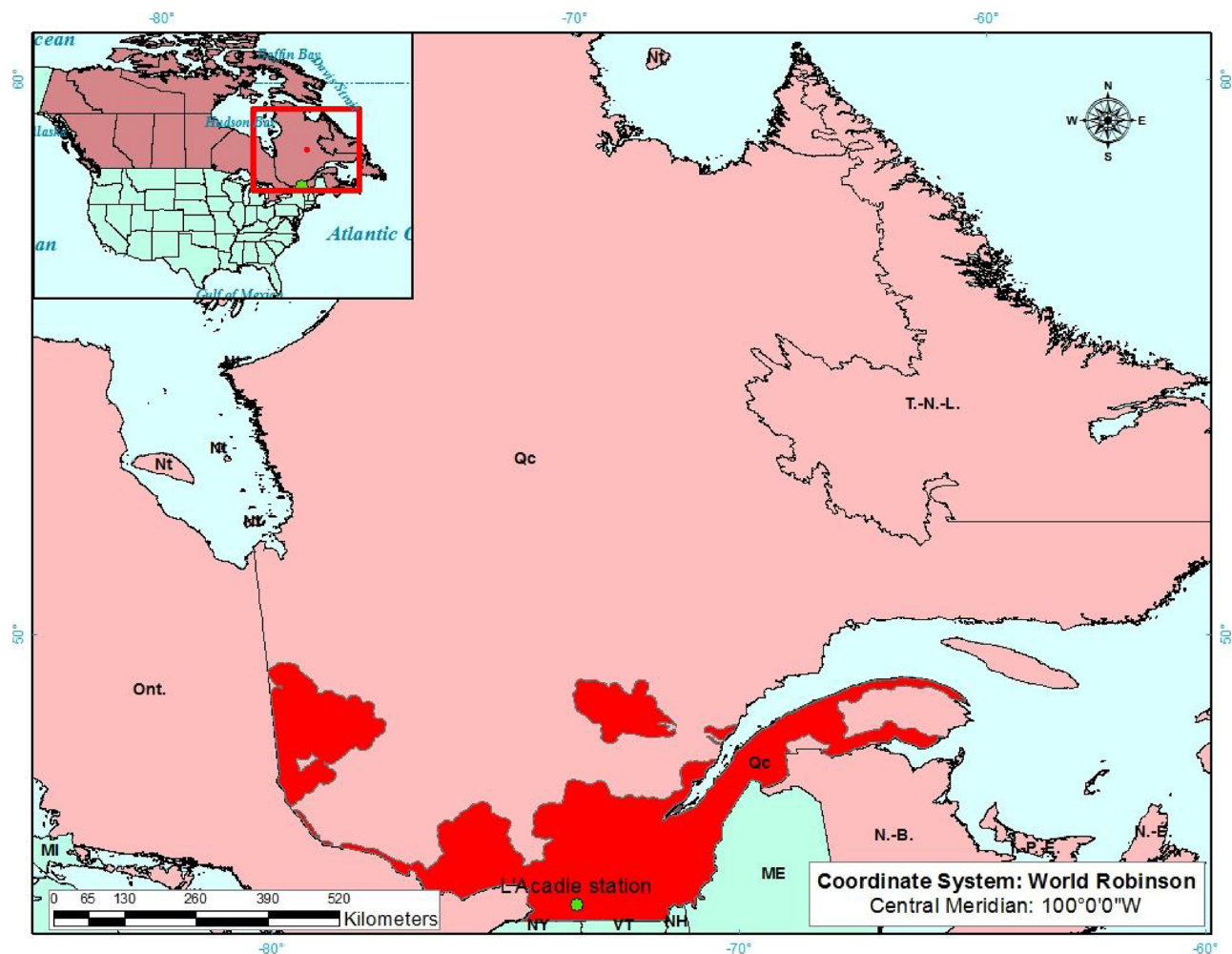
The climate models simulating the 2050 horizon were developed by the OURANOS climate scenarios team (Roy, P., unpublished). Climate simulations were adjusted by a method of “quantile - quantile mapping” (Thiemeßl et al., 2011) that allows to correct the bias of a simulation. This method finds the quantiles of model variables and substitutes the simulated values with those of the identical quantile from an observational dataset. To obtain a good resolution, AAFC's 10 km x 10 km grid was used for the development of soybean and SCN phenology models (Hutchinson, 2004; Hutchinson et al., 2009).

Daily air temperatures recorded over a 30-year period (1981–2010) in Québec and those simulated for the 2050 horizon have been integrated in a software developed by AAFC's bioclimatology and modelling research team (Plouffe et al., 2014). Daily soil temperatures were estimated using a number of equations available in the STICS (“Simulateur multIdisciplinaire pour les Cultures Standard”) crop growth and development simulator (Brisson et al., 2008). Air temperature data were used for the soybean phenology model and soil temperature at 20-cm depth for the SCN phenology model since nematodes are more abundant in the first layer of soil between 0 and 20 cm (Alston and Schmitt, 1987).

Optimistic (cooler) and pessimistic (warmer) scenarios have been developed to illustrate the inter-annual variation between simulations within each RCP. For each variable, the ten climate models were run. Only the values obtained by at least 9/10 models in at least 24/30 years were kept. The 10th and 90th percentile values were identified in each climate model output. The average of all the 10th percentile values was reported as the “warmer scenario” and represents the higher temperature while the average of the 90th percentile values was the “cooler scenario” and represents the lower temperature of the distribution. This allows the quantification of the uncertainty associated with the projections for the 2050 horizon.

Bioclimatic models simulating soybean and SCN phenology as a function of photoperiod and air and soil temperature

The model simulating soybean phenology as a function of air temperature and photoperiod was provided by AAFC's bioclimatology and modelling research team in Saint-Jean-sur-Richelieu, Québec (Plouffe et al., 2014). In summary, thirty data sets obtained over four years, two sites, and multiple planting dates, were used for model conceptualization and calibration. A series of equations are associated to three specific phenological phases of the plant, namely emergence, vegetative and reproductive phases. Equations within each phenological phase include effects of both temperature  $f(T)$  and photoperiod  $f(P)$ . The temperature and photoperiod functions originate from Yan and Hunt (1999) and Setiyono et al. (2010), respectively (see Supplementary Material S1 for more details). This phenology model was incorporated in CIPRA (Computer centre for agricultural pest forecasting) software



**Fig. 1.** Study zone in red of Québec province representing the extent of the agricultural land. The L'Acadie research station of Agriculture and Agri-Food Canada is identified by a green dot (Basemap belong to ArcGIS® software by ESRI).

**Table 1**  
List of ten climate models from the CMIP5 (2015) used in the construction of the RCP4.5 and RCP8.5 climate change simulations.

Modelling Center	Model	Institution	Reference
CSIRO-BOM	ACCESS1-0	CSIRO (Commonwealth Scientific and Industrial Research Organisation, Australia), and BOM (Bureau of Meteorology, Australia)	Collier et Uhe, 2012.
CNRM-CERFACS	CNRM-CM5	Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancées en Calcul Scientifique	Voldoire et al., 2011.
CSIRO-QCCCE	CSIRO-Mk3-6-0	Commonwealth Scientific and Industrial Research Organisation in collaboration with the Queensland Climate Change Centre of Excellence	Gordon et al., 2010.
NOAA GFDL	GFDL-ESM2G	Geophysical Fluid Dynamics Laboratory	Dunne et al., 2012, 2013.
IPSL	IPSL-CM5A-MR	Institut Pierre-Simon Laplace	Dufresne et al., 2013.
MIROC	MIROC5	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology	Watanabe et al., 2010.
MPI-M	MPI-ESM-MR	Max Planck Institute for Meteorology (MPI-M)	Giorgetta et al., 2013.
NCC	NorESM1-M	Norwegian Climate Centre	Bentsen et al., 2013.
INM	INMCM4	Institute for Numerical Mathematics	Volodin et al., 2010.
CCCma	CanESM2	Canadian Centre for Climate Modelling and Analysis	Chylek et al., 2011.

(Plouffe et al., 2014). The map describing potential growing area for soybean in Québec was generated using the soybean phenology model for the reference period and the 2050 horizon. Soybean maturity group I (MG-I), currently sowed in Québec, was used in the model. Maps were produced using ArcMap 10.3.

The development of SCN phenology model was based on a mechanistic approach that uses species-specific physiological tolerance factors such as temperature to predict its developmental rate (Jeschke

and Strayer, 2008). Developmental data measurements such as stage duration for temperatures between 16 °C and 32 °C were obtained from the literature (Ross, 1964; Lauritis et al., 1983; Melton et al., 1986). Because growth rates differed between eggs (in the soil) and other developmental stages (in soybean roots), two equations were developed. A linear regression was used to describe the growth of SCN inside the egg, from embryogenesis to hatching of the second juvenile stage (J2), for temperatures between 16 °C and 30 °C.



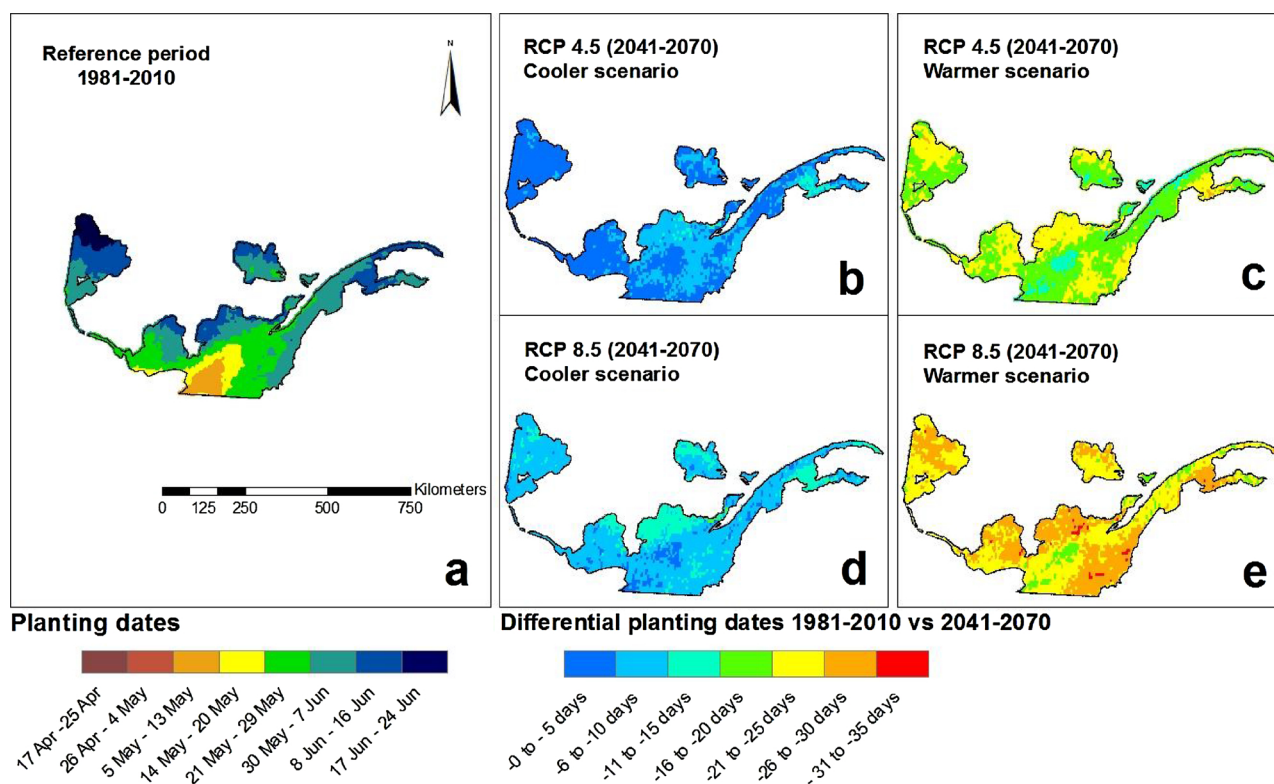


Fig. 2. Differences between future and reference planting dates for soybean MG-I in Québec, based on greenhouse gases concentration pathway simulations RCP 4.5 and 8.5. Cooler and warmer scenarios represent the inter-annual variation obtained by 10 different climate simulations within each RCP. The cooler scenario is the average of the 10th percentile values obtained using each of the models and represents the lower temperatures of the distribution while the warmer scenario is the mean of the 90th percentile values, representing the higher temperature obtained across the 30 years. Negative values indicate planting dates earlier than the reference period (1981–2010).

$$Y = 0.0041x + 0.0087 \quad (\text{A.1})$$

$Y$  represents the number of days to reach the J2 stage and hatch and  $x$  is the temperature in Celsius degrees. Then, a polynomial regression described the growth of SCN following penetration of the root (from J2 to adult) for temperatures between 16 °C and 32 °C.

$$Y = 0.0008x^2 + 0.04x - 0.4106 \quad (\text{A.2})$$

$Y$  represents the number of days to reach the adult stage and  $x$  is the temperature in Celsius degrees.

In order to simplify the model, we made three important assumptions (reviewed in Jeschke and Strayer, 2008). First, biotic interactions do not influence positively or negatively SCN geographical range over space and time. Second, the genetic and phenotypic compositions of SCN populations are constant over space and time. Third, SCN can disperse wherever its hosts are present, i.e. in this study, where soybean is grown. Of course, biotic interactions can influence SCN dispersal and host susceptibility, this will need to be addressed in future studies.

The SCN phenology model starts with SCN egg hatching which is set to the same day than the predicted soybean sowing date; this in order to simplify the model but also to synchronize SCN life cycle with the presence of the host. Since the soybean planting date varies with years, it is estimated using an algorithm. The algorithm first identifies the median date of the last spring frost for each geographic node (10 km x 10 km) and related depth (20 cm) using reference climate datasets (1981–2010) or datasets generated by the two RCP scenarios. Then, for each year, starting on the median date of the last spring frost, the software identifies a moving 5-day mean temperature greater than or equal to 12.8 °C. Under this temperature, the soybean seeds develop very slowly and can enter dormancy (Ontario Ministry of Agriculture Food and Rural Affairs OMAFRA (2009)). The fifth day corresponds to the planting date used in the model.

As parameters associated with SCN reproduction, including migration of the males out of the root to mate with the females, are complex and difficult to include in the model, three days were added to the model after the adult stage is reached and prior to embryogenesis based on migration approximation made by Lauritis et al. (1983). The model provides the dates on which the embryonic (four cells to first juvenile stage (J1)), infectious (J2) and adult stages are reached, the duration of each stage, and the number of generations per growing season. The last seasonal SCN generation was considered incomplete if the adult stage is not reached in at least 24 years out of 30 years with a predicted value in at least nine of the ten climate models.

### 2.3. Calculation of key variables

Using the parameters described above, the soybean planting date is calculated for each geographic node (10 km x 10 km) using the ten climate models. Then, each simulation predicts the date when each soybean phenological stage is reached using degree-day accumulation. The average of the 10th and 90th percentile values obtained using each of the ten climate models was reported as the “cooler” and “warmer” scenarios for planting and maturity dates at each of the geographic node. In the same manner, the completion of each SCN developmental stage was calculated using the equations described above starting at the planting date predicted by each of the ten climate models. The number of full generations by growing season is reported for future and reference climate for each of the geographical node. The duration (days) and dates associated with the beginning and the end of each generation was also outputted for the geographical node corresponding to L’Acadie experimental station. The inter-annual variation was also evaluated by averaging the 10th and 90th percentile values obtained by each of the ten climate models. ArcMap 10.3 was used to produce maps illustrating

the number of generations potentially produced in the climatic conditions of the reference period (1981–2010) and of the 2050 horizon. All these variables were calculated under both RCP simulations.

### 3. Results

#### 3.1. Soybean phenology under different greenhouse gases concentration trajectories

The differences between soybean maturity group I planting dates in Québec depending on RCP simulations and climate change scenarios are shown in Fig. 2.

Under the reference scenario (1981–2010), soybean can be planted from May 5<sup>th</sup> in southern Québec to June 24<sup>th</sup> in the northern area (Fig. 2a). During the 2050 horizon, models predicted that under the greenhouses concentration pathway of RCP 4.5, it will be possible to plant soybean up to 15 days earlier under a cooler scenario (Fig. 2b) and up to 25 days earlier under a warmer scenario (Fig. 2c). For RCP 8.5, models suggested that soybean could be sowed up to 15 days earlier under a cooler scenario (Fig. 2d) and up to 35 days earlier under a warmer scenario (Fig. 2e).

Fig. 3 shows the potential for MG-I soybean to reach maturity currently (Reference period) and under RCP simulations.

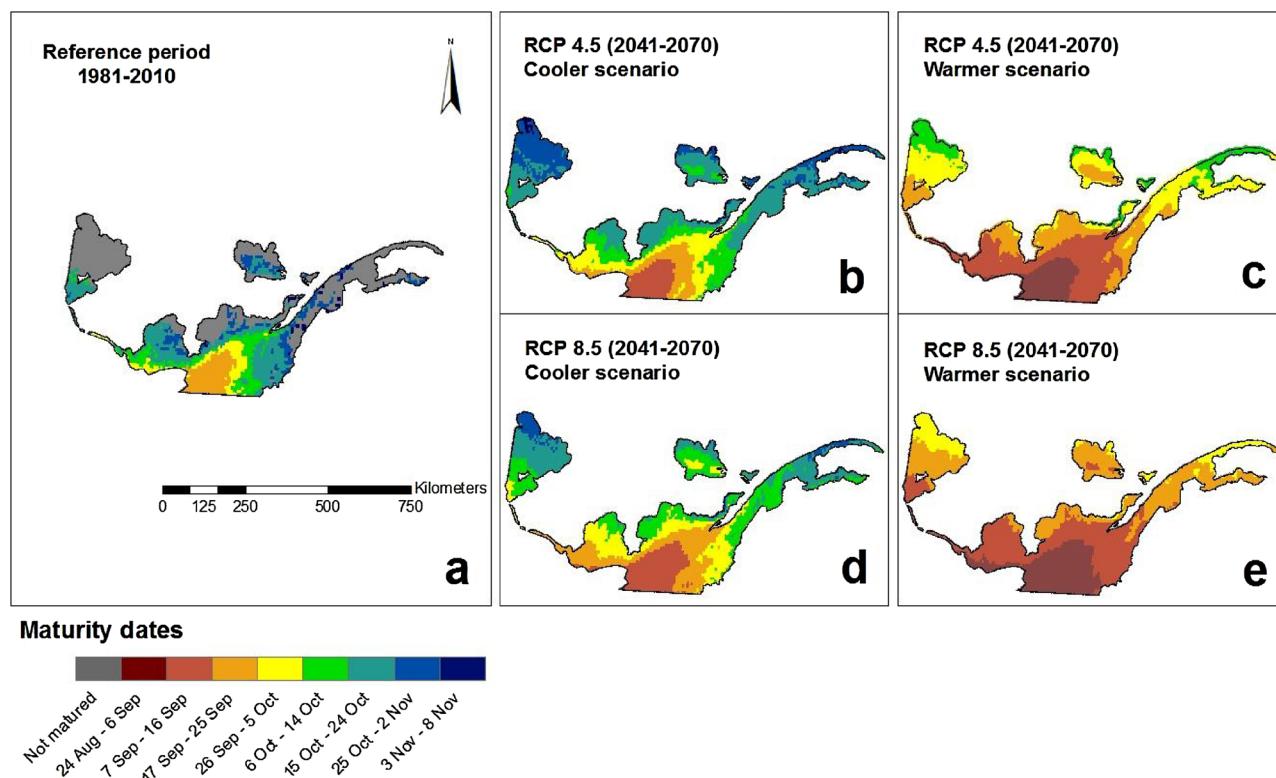
Soybean (MG-I) maturity during the 1981–2010 period can be reached from late September in south-western Québec to late October in other areas (Fig. 3a). The models predicted that soybean could be harvested from September 7<sup>th</sup> (south) to November 9<sup>th</sup> (north) under the cooler scenario of RCP 4.5 simulations (Fig. 3b). Harvesting will start sooner, from August 24<sup>th</sup> (south) to mid-October (north), under a warmer scenario (Fig. 3c). Thus, it will be possible to harvest 14 days earlier in southern Québec under a warmer scenario and 25 days earlier in the north. Under the cooler scenario of RCP 8.5 simulations (Fig. 3d),

the model predicted that soybean could be harvested from September 7<sup>th</sup> to November 2<sup>nd</sup> from south to north, respectively, whereas under a warmer scenario (Fig. 3e) this period will start as soon as August 24<sup>th</sup> to October 5<sup>th</sup> from south to north, respectively when comparing the warmer and the cooler scenario, the models predicted that in the south it will be possible to harvest up to 14 days earlier while in the north harvest could occur up to 28 days earlier.

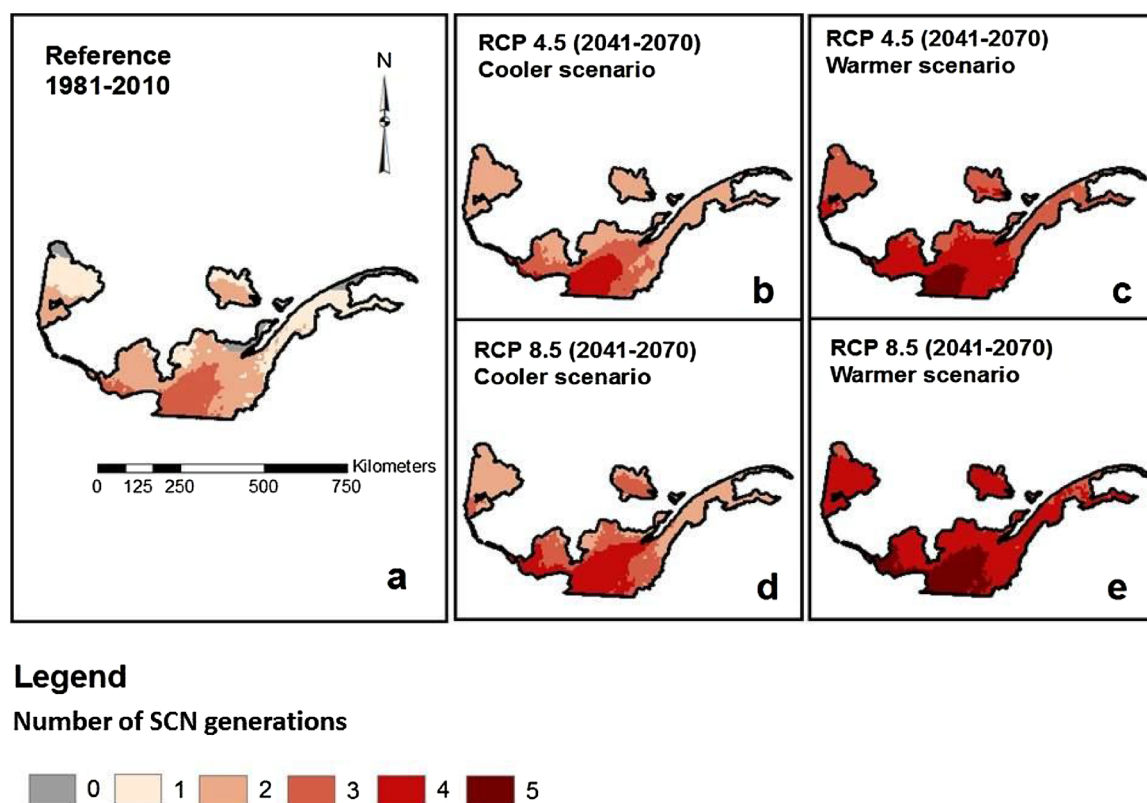
#### 3.2. Predicted number of SCN generations during a growing season over Québec cropland

In order to figure out SCN reproductive potential at 20 cm depth in Québec's cropland, the total number of SCN generations produced during a single season was mapped for the reference period and RCP's simulations of future climate (Fig. 4).

From the reference period to the 2050 horizon, there will be a marked increase in the number of SCN generations produced over a growing season. Currently, up to three generations can be obtained in the area where soybean is grown (Fig. 4a) and SCN cannot survive or attain sexual maturity in the northern limits of Québec's cropland. In contrast, both RCP simulations indicate that future climatic conditions could allow the development of additional SCN generations. Modelling of SCN phenology using RCP 4.5 simulations under the cooler scenario (Fig. 4b) predicted the completion from four (south) to two (north) generations while under a warmer scenario it predicted the completion from five (south) to two (north) generations. Under the cooler scenario simulated with the RCP 8.5 data (Fig. 4d), the number of expected full generations is similar to RCP 4.5 results, with the exception that the area where five and four generations could be completed is much larger. Finally, the warmer scenario simulated with RCP 8.5 (Fig. 4e), predicted the completion of five generations over a larger area in southern Québec, four generations almost everywhere else, except at



**Fig. 3.** Soybean (MG-I) maturity dates (mean values) under the reference period and the 2050 horizon in Québec based on greenhouse gases concentration pathway RCP 4.5 and 8.5. Cooler and warmer scenarios represent the inter-annual variation obtained by 10 different climate simulations within each RCP. The cooler scenario is the average of the 10th percentile values obtained using each of the models and represents the lower temperatures of the distribution while the warmer scenario is the mean of the 90th percentile values, representing the higher temperature obtained across the 30 years. Maturity is not reached in grey areas.



**Fig. 4.** Number of soybean cyst nematode generations completed at 20 cm depth during a single growing season in Québec for the reference period and the 2050 horizon using two RCP simulations. Cooler and warmer scenarios represent the variation between simulations within each RCP. For the 2050 horizon, generations had to be completed for at least 24 years over 30 to be recorded.

the northern limits where three generations could be completed.

### 3.3. SCN seasonal population dynamics: a case scenario at L'Acadie station

To illustrate the application of the model on expected seasonal population dynamics of SCN, we selected an experimental site located at L'Acadie (45°17'38" N, 73°20'58" W, 4380 m), in the middle of the main soybean production area in Québec, and where weather data are available for the past 30 years. Fig. 5 illustrates the predicted number and duration (from embryogenesis to adult) of SCN generations based on the average of the 10 climate models for the reference period and 2050 horizon and classified into optimistic (cooler) and pessimistic (warmer) scenarios.

Modelling suggested that soybean can currently be sowed around May 12th and that SCN can complete three generations from mid-May to the end of August in southern Québec (Fig. 5, blue gradient). Nematodes most likely enter into winter dormancy between the end of August and September 25th without completing a fourth generation 20 years out of 30.

With the expected increase in temperatures in the 2050 horizon, under the RCP 4.5 planting dates of soybean MG-I (Fig. 5) under a warmer scenario could be advanced by 16 days compared to the cooler scenario. The duration of interaction (synchronism) between soybean MG-I and SCN populations is similar in both scenarios, but under a warmer climate nematodes could pursue their development even in absence of its host for about a month. SCN developmental and reproductive period could last 140 and 162 days under the cooler and warmer scenario, respectively. RCP 4.5 simulations under the cooler (Fig. 5, lower yellow gradient) and warmer (Fig. 5 upper yellow gradient) scenario predicted four and five complete generations, respectively.

Under the RCP 8.5, the planting date under a warmer scenario will

be advanced by 19 days compare to the cooler scenario. SCN potential reproductive period varied from 146 days under a cooler scenario to 187 days under a warmer scenario. The RCP 8.5 simulations under the cooler scenario (Fig. 5, lower red gradient) predicted four complete generations and the initiation of a fifth incomplete generation. Under the warmer scenario (Fig. 5, upper red gradient), five complete generations are predicted with the completion of a sixth generation 13 years out of 30.

During the 2050 horizon, soybean planting date will be between 5 to 21 days (RCP 4.5) and 8 to 27 days (RCP 8.5) earlier. The duration of interaction between soybean and SCN (from 128 to 138 days) is similar for each scenarios and periods, but under a warmer climate the nematode could pursue its development from about 50 more days. SCN potential reproductive period will be between 4 to 26 days (RCP 4.5) and 10 and 51 day (RCP 8.5) longer during the 2050 horizon. Finally, temperature change during the 2050 horizon could lead to the production of one to two additional generations of SCN.

## 4. Discussion

This study showed that climate change would modify host and parasite phenology and population dynamics. Climate warming will change soybean production in northern latitude by lengthening the growth season and opening new areas to this crop. Concurrently, higher temperatures will also increase the rate of development of SCN, a poikilothermic species.

### 4.1. Growing soybean under climate change in the province of Québec

Phenology modelling for the 2050 horizon predicted a significant increase in the potential soybean growing area (Figs. 2 and 3) and earlier planting dates in all regions where soybean is currently grown.



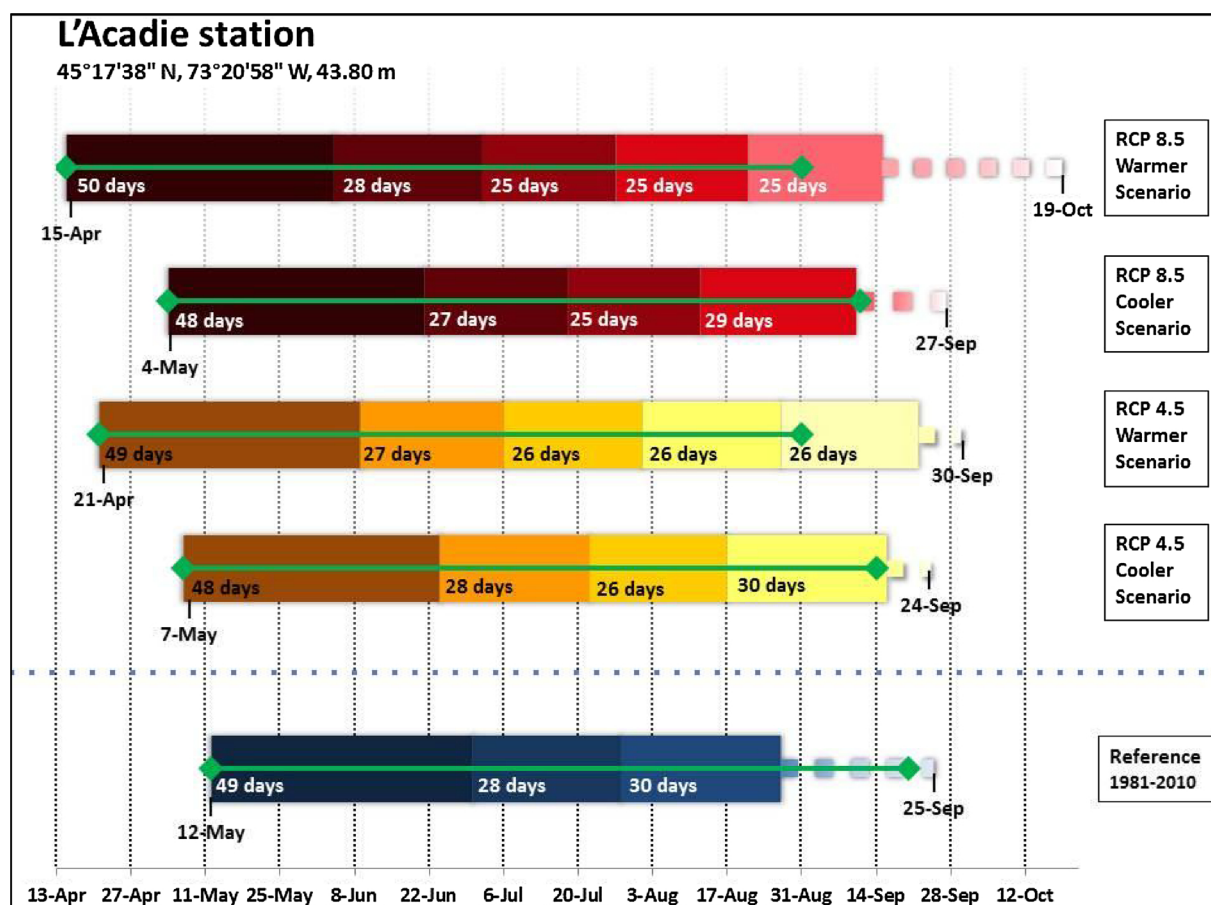


Fig. 5. Duration (days) and dates associated with the beginning and the end of each generation of soybean cyst nematode completed during a growing season for the reference period and the 2050 horizon at L'Acadie experimental station, Québec. Dotted lines to the right of each bar represent incomplete generation at the end of the season. Blue, yellow and red gradient bar represent the reference period, the RCP 4.5 and the RCP 8.5, respectively. For each RCP, the bottom and upper bars represent the cooler (90th percentile) and warmer (10th percentile) scenarios, respectively. Green lines represent soybean MG-I cropping cycle based on predicted sowing and maturity dates obtained by the 10 climatic simulations.

Predictions showed that soybean MG-I could currently be grown all over the existing cultivable land in Québec. Depending on the RCP simulation and latitude, temperature increase associated with climate change could extend the soybean growing season by one to three weeks for the 2050 horizon as Bootsma et al. (2005) demonstrated in their study. According to our results, a shift in MG will likely occur in all regions. For example, for regions in southern parts of the cultivable land, where MG-I soybean is currently grown, the model predicted an earlier planting date. Because soybean growth and development will benefit of longer days (daylight reach its maximum at end of June then start decreasing), planting MG-II soybean could be successful. As demonstrated in other studies, early planting generates higher yields because soybean reproduction starts sooner when days are longer and light is more intense (Zhang et al., 2000; De Bruin and Pedersen, 2008; Nafzinger, 2009; Robinson et al., 2009). Therefore, a favourable temperature scenario such as RCP 4.5 or RCP 8.5 where soybean could be planted in southern area in early April rather than in early May would provide growers more seeds per plant. However, the consequences of early planting on pest population dynamics also need to be considered.

#### 4.2. Possible effects of climate change on SCN seasonal cycle

The genetic variability and adaptation potential towards climate change of SCN populations established in Québec remain to be explored. Understanding the capacity of the species to adapt to current and future climate is critical to forecast colonization of new areas, as it was shown in North America for other pathogens, insects and weeds

(Boland et al., 2004; Dukes et al., 2009, 2011; Urbanski et al., 2012; Baker et al., 2015). All RCP simulations predicted an increase of the number of generations of SCN during the growing season from currently three to potentially four or five. As for its plant host, warming alone will accelerate SCN development. This species should therefore become more abundant in Québec, as for the United States of America and South America where warmer climate and longer presence of the host provide ideal conditions for its reproduction (Tylka and Marett, 2014). Under the different latitudinal climate and field conditions from Florida to North Dakota, SCN can produce from six to two generations by growing season University of Illinois at Urbana-Champaign (1991; Nelson and Bradley, 2003; Iowa State University, 2004; Chen, 2011). These results are consistent with SCN life cycle models run with future temperature data that are predicting four to five (RCP 4.5) or five to six generations (RCP 8.5). These comparisons showed that the model seems consistent with the situation currently observed in southern areas and could help Québec growers to anticipate and manage this pest species under future climate.

Together, the rise of temperature and the expected increase of the soybean growing area could influence and enlarge the establishment area and the distribution of SCN across the province of Québec. Similar situation has occurred in Minnesota where SCN has spread at the same rate as soybean production increased from south to north since the first discovery of SCN in 1978 (Chen, 2011; Kendel (2013)). Simulation of SCN development showed that SCN could currently complete its life cycle in all the cultivable lands in Québec if a susceptible host is available. For now, SCN has been found in different region of southern

Québec where MG-000 to MG-I soybean are grown (Mimee et al., 2016). RCP simulations suggest that SCN infestations at higher latitudes, on MG-000 to MG-0, would considerably complicate its management as most of the available resistant cultivars have been developed for higher maturity groups (Orf, 2013; Rincker et al., 2017). Thus, it is very important to anticipate the establishment of SCN populations at higher latitudes by increasing the breeding efforts for SCN resistance in short season soybean and diversifying the sources of resistance.

For a better understanding of the effects of climate changes on SCN life cycle at a farm scale level, a case study was run at a specific location in Québec's main soybean growing area. Simulations predicted significant effects of climate change on soybean phenology and SCN development at L'Acadie, with earlier planting dates (between 5 to 27 days) in the near future. This could allow a shift in maturity groups from MG-I to MG-II with longer vegetative stage duration. Despite the earlier arrival of higher temperatures, the duration of SCN first generations will not be shorter because the cycle will begin sooner, the temperatures will still be low and SCN developmental rate should remain the same during the first generation. On the other hand, summer temperatures will be near optimal and should accelerate the rate of development. However, a shift to MG-II would extend the presence of soybean vegetative stage in the field by 5–20 days. This could allow secondary infections during this stage and limit root growth (Jiang and Egli, 1995; Pederson et al., 2008). The resulting damages would significantly impair subsequent flowering and pod filling which are critical stages for yield (Wrather and Anand, 1988; Todd, 1993). Currently, soybean plants from MG-I grown at L'Acadie station take about 40 to 43 days to reach flowering and the duration of the first SCN generation is 49 days. Hence, only the initial generation (spring inoculum) invades the roots and limit water and nutrient intakes during this stage.

After flowering, the modelling of soybean MG-I planted at L'Acadie station predicted that the reproductive stage will last for 68–72 days. This stage is critical for yield determination in terms of seed number and pod size. Moreover, SCN could still impair directly and indirectly production by weakening the plant and increasing damages by other diseases like the fungi causing the Sudden Death Syndrome (SDS) and others such as members of the oomycetes (Todd et al., 1987; Wang et al., 2003). Furthermore, RCP simulations predict more generations from mid-summer to fall which could lead to increases in SCN population density and cyst number that will constitute the initial inoculum of the next growing season.

As seen previously in RCP simulations, SCN can pursue its development during more than one month after its host had reached maturity, which can be enough to produce a fifth or a sixth complete generation. These ultimate generations will not directly impact the soybean because at this stage pod production is over but could lead to an increased inoculum that will affect soybean production the following year. In addition, the presence of winter annual weeds such as purple deadnettle (*Lamium purpureum*) or common chickweed (*Stellaria media*), both excellent alternative host which are present in Québec, could allowed a greater production of cyst as seen in United States and augment the annual inoculum (Johnson et al., 2008). Altogether, the longer growth season and the presence of winter weeds as the potential to impede significantly the soybean production in Québec in a context of climate change.

#### 4.3. Bioclimatic modelling and climate change

In this study we developed a process-based SCN phenology model relying only on the literature available describing the relationship between temperature and SCN development to describe the effect of climate warming on a soil temperature dependent nematode species without considering the effect of other bioclimatic and abiotic factors that could also influence its development. Nevertheless, our study demonstrates that the use of daily fluctuating temperature data coupled with a simple mathematical equation were sufficient to simulate the

development and reproduction of a soil species from embryogenesis to sexual maturity and egg laying. This model still needs to be validated with field trials under different temperature regimes; however, when compared with different locations across the United States of America, the number of generations produced during one growing season is realistic. The approach also innovates by combining the phenology of the host to the temperature-based modelling of pest development. This greatly increases the outcomes of modelling by highlighting the synchronism of different stages and predicting if the pest will attack the plant during a more susceptible or yield-limiting stage. It also allows the computation of indirect effects of climate on pest development such as the presence of the host or not. We consider that this type of simplistic model would help anticipate the potential impact of a pest species and to plan future management of crop and pest control based on potential needs. It is also easily adaptable to other plant-parasite systems as it does not rely on complex parameters of crop growth simulations. In this study, the two chosen RCPs all predicted a global rise of temperatures, sea levels, precipitations and others environmental variables so that the biology of all poikilothermic species could dramatically change in the near future.

To our knowledge, this is the first mechanistic bioclimatic and coupled host-pest phenology model for the prediction of current and future SCN distribution and reproduction potential under different climatic scenarios. Soybean acreages have exploded in Canada during the last decade and will continue to increase. The recent introduction of SCN in Québec has generated a lot of concerns for growers and raised important questions about its potential of establishment in the province. With this regard, the development of a simple and realistic model that could be used in any climatic region to quickly enable authorities to determine the reproductive potential of SCN was the first step of an integrated crop-pest management program.

#### 4.4. Future perspectives

The perspective of a warming climate can be seen as a good opportunity for northern agriculture. This would open up new lands to lucrative crops like soybean and extend the growing season in the current production area, allowing the planting of late maturity cultivars with higher yields. However, this will indubitably have major consequences on pests and diseases as already suggested in numerous studies (Bebber et al., 2013; Elad and Pertot, 2014; Kistner, 2017). Many organisms are currently unable to overwinter or have very limited impact under the current climate and could become problematic in future. For SCN, this study has also shown that a shift to MG-II would extend the presence of the host vegetative stage and allow more secondary infections that could negatively impact yield. The shorter SCN developmental time under warmer climate will also accelerate the build-up and spread of nematode populations that could also be facilitated by an increase in soybean cultivated areas and better connectivity between fields. Therefore, it is crucial to develop and deploy new pest management tools to maximize the chances of a positive outcome. We have to develop cultivars integrating novel sources of resistance. We can also imagine the development of a predictive yield model that integrates winter survival, inoculum density and, eventually, interactions with other biotic and abiotic factors in each region. This information would help the growers to make a conscious choice of cultivar and MG to maximize their profits in a changing climate.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.10.008>.

## References

- Agriculture and Agri-Food Canada (AAFC), 2015. Quebec Agroclimatic Atlas Data. Retrieved from. [Nov 2017]. <http://open.canada.ca/data/en/dataset/03807263-b1ad-44e9-b2a9-b574cd26e992>.
- Alston, D.G., Schmitt, D.P., 1987. Population density and spatial pattern of *Heterodera glycines* in relation to soybean phenology. *J. Nematol.* 19, 336–345.
- Anderson, J.P., Badruzaufari, E., Schenk, P.M., Manners, J.M., Desmond, O.J., Ehler, C., Maclean, D.J., Ebert, P.R., Kazan, K., 2004. Antagonistic interaction between abscisic acid and jasmonate-ethylene signaling pathways modulates defense gene expression and disease resistance in *Arabidopsis*. *Plant Cell* 16, 3460–3479.
- Anderson, T.R., Welacky, T.W., 1988. First report of *Heterodera glycines* on soybeans in Ontario, Canada. *Plant Dis.* 72, 453.
- Baker, M.B., Venugopal, P.D., Lamp, W.O., 2015. Climate change and phenology: *Empoasca fabae* (Hemiptera: Cicadellidae) migration and severity of impact. *PLoS One* 10, e0124915.
- Bhattarai, M.D., Secchi, S., Schoof, J., 2017. Projecting corn and soybeans yields under climate change in a corn belt watershed. *Agric. Syst.* 152, 90–99.
- Bebber, D.P., Ramotowski, M.A.T., Gurr, S.J., 2013. Crop pests and pathogens move polewards in a warming world. *Nat. Clim. Change* 3, 985–988.
- Bentsen, M., Bethke, I., Debernard, J.B., 2013. The Norwegian earth system model, NorESM1-M – part 1: description and basic evaluation of the physical climate. *Geosci. Model Dev.* 6, 687–720.
- Boland, G.J., Melzer, M.S., Hopkin, A.A., Higgins, V., Nassuth, A., 2004. Climate change and plant diseases in Ontario. *Can. J. Plant Pathol.* 26, 335–350.
- Bonner, M.J., Schmitt, D.P., 1985. Population dynamics of *Heterodera glycines* life stages on soybean. *J. Nematol.* 17, 153–158.
- Bootsma, A., Gameda, S., McKenney, D.W., 2005. Potential impacts of climate change on corn, soybeans and barley yields in Atlantic Canada. *Can. J. Plant Sci.* 85, 345–357.
- Brisson, N., Launay, M., Mary, B., Beaudoin, N., 2008. Conceptual Basis, Formalisations and Parameterization of the STICS Crop Model. INRA, Versailles, France Éditions Quae, 297 p.
- Chen, S., 2011. Soybean cyst nematode management guide. Cyst Nematode Management Guide, 2008. University of Minnesota Extension Retrieved from. <http://www1.extension.umn.edu/agriculture/soybean/soybean-cyst-nematode/> [Nov 2017].
- Coupled Model Intercomparison Project Phase 5 (CMIP5), 2015. CMIP5 - Data Access - Availability. Retrieved from. [Nov 2017]. <http://cmip-pcmdi.llnl.gov/cmip5/availability.html>.
- Chylek, P., Li, J., Dubey, M.K., Wang, M., Lesins, G., 2011. Observed and model simulated 20th century Arctic temperature variability: Canadian earth system model CanESM2. *Atmos. Chem. Phys. Discuss.* 11, 22893–22907.
- Collier, M., Uhe, P., 2012. CMIP5 Datasets from the ACCESS1.0 and ACCESS1.3 Coupled Climate Models. CAWCR Technical Report No. 059. The Centre for Australian Weather and Climate Research. Retrieved from. Aspendale, Victoria. <http://citeserxist.psu.edu/viewdoc/download?doi=10.1.1.710.4998&rep=rep1&type=pdf>.
- De Bruin, J.L., Pedersen, P., 2008. Soybean seed yield response to planting date and seeding rate in the Upper Midwest. *Agron. J.* 100, 696–703.
- Donnatelli, M., Magarey, M.D., Bregaglio, S., Willocquet, L., Whish, J.P.M., Savary, S., 2017. Modelling the impacts of pests and disease on agricultural systems. *Agr. Syst.* 155, 213–224.
- Dukes, J.S., Chiariello, N.R., Loarie, S.R., Field, C.B., 2011. Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes. *Ecol. Appl.* 21 (6), 1887–1894.
- Deutsch, C.A., Tewksbury, J.J., Tigchelaar, M., Battisti, D.S., Merrill, S.C., Huey, R.B., Naylor, R.L., 2018. Increase in crop losses to insect pests in a warming climate. *Science* 361 (6405), 916–919.
- Dukes, J.S., Pontius, J., Orwig, D., Garnas, J.R., Rodgers, V.L., Brazee, N., et al., 2009. Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: what can we predict? *Can. J. For. Res.* 39, 231–248.
- Dufresne, J.L., Foujols, M.A., Denvil, S., Caubel, A., Marti, O., Aumon, O., et al., 2013. Climate change projections using the IPSL-CM5 earth system model: from CMIP3 to CMIP5. *Clim. Dyn.* 40, 2123–2165.
- Dunne, J.P., John, J.G., Adcroft, A.J., Griffies, S.M., Hallberg, R.W., Shevliakova, E., et al., 2012. GFDL's ESM2 global coupled climate-carbon earth system models. Part I: physical formulation and baseline simulation characteristics. *J. Clim.* 25, 6646–6665.
- Dunne, J.P., John, J.G., Shevliakova, E., Stouffer, R.J., Krasting, J.P., Malyshev, S.L., et al., 2013. GFDL's ESM2 global coupled climate-carbon earth system models. Part II: carbon system formulation and baseline simulation characteristics. *J. Clim.* 26, 2247–2267.
- Elad, Y., Pertot, I., 2014. Climate change impacts on plant pathogens and plant diseases. *J. Crop Improv.* 28, 99–139.
- FAO, 2017. The future of food and agriculture. Retrieved from. Trends and challenges, Rome [Dec 2017]. <http://www.fao.org/3/a-i6583e.pdf>.
- FAOSTAT, 2017a. 2014 World Area Harvested of Primary Crops. Retrieved from. [Oct 2017]. <http://faostat.fao.org>.
- FAOSTAT, 2017b. 2014 World Production Quantity of Primary Crops. Retrieved from. [Oct 2017]. <http://faostat.fao.org>.
- Giorgetta, M.A., Roeckner, E., Mauritsen, T., Bader, J., Crueger, T., Esch, M., et al., 2013. The Atmospheric General Circulation Model ECHAM6: Model Description (Report N°135). Retrieved from. Max Planck Institute for Meteorology, Hamburg [Sep 2016]. [https://www.mpimet.mpg.de/fileadmin/publikationen/Reports/WB\\_BzE\\_135.pdf](https://www.mpimet.mpg.de/fileadmin/publikationen/Reports/WB_BzE_135.pdf).
- Gordon, H., O'Farrell, S., Collier, M., Dix, M., Rotstayn, L., Kowalczyk, E., et al., 2010. The CSIRO Mk3.5 climate model. CAWCR Technical Report No. 021. The Centre for Australian Weather and Climate Research, Melbourne, Victoria Retrieved from. [http://www.cawcr.gov.au/technical-reports/CTR\\_021.pdf](http://www.cawcr.gov.au/technical-reports/CTR_021.pdf) [Sep 2016].
- Gruke, N.E., 2011. The nexus of host and pathogen phenology: understanding the disease triangle with climate change. *New Phytol.* 189, 8–11.
- Hutchinson, M.F., 2004. ANUSPLIN Version 4.3. Retrieved from. Australian National University, Canberra [Nov 2017]. <https://researchers.anu.edu.au/publications/38018?term=anusplin+4.3>.
- Hutchinson, M.F., McKenney, D.W., Lawrence, K., Pedlar, J.H., Hopkinson, R.F., Milewska, E., Papadopol, P., 2009. Development and testing of Canada-wide interpolated spatial models of daily minimum–maximum temperature and precipitation for 1961–2003. *J. Appl. Meteorol. Climatol.* 48, 725–741.
- Interpanel on Climate Change (IPCC) 2014. Climate Change 2014: Synthesis Report. In: Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Eds. Core writing team, Pachauri, R.K. & Meyer, L. A.). Geneva, Switzerland, 151.
- Jeschke, J.M., Strayer, D.L., 2008. Usefulness of bioclimatic models for studying climate change and invasive species. *Ann. N. Y. Acad. Sci.* 1134, 1–24.
- Jiang, H., Egli, D.B., 1995. Soybean seed number and crop growth rate during flowering. *Agron. J.* 87, 264–267.
- Johnson, W.G., Creech, J.E., Mock, V.A., 2008. Role of winter annual weeds as alternative hosts for soybean cyst nematode. *Crop Manage.* 7, 1–9. <https://doi.org/10.1094/CM2008-0701-01-RV>.
- Kendel, H., 2013. Soybean production – Field guide for North Dakota and Northwestern Minnesota (Guide A-1172). Retrieved from. North Dakota State University Extension Service, Fargo [Nov 2017]. <https://www.ag.ndsu.edu/publications/landing-pages/crops/soybean-production-guide-a-1172>.
- Kistner, E.J., 2017. Climate change impacts on the invasive brown marmorated stink bug. United States Department of Agriculture – Midwest Climate Hub. Retrieved from. [http://www.petrisk.org/wp-content/uploads/2017/10/3\\_3\\_IPRRG11\\_Kistner.pdf](http://www.petrisk.org/wp-content/uploads/2017/10/3_3_IPRRG11_Kistner.pdf) [Dec 2017].
- Lauritis, J.A., Rebois, R.V., Graney, L.S., 1983. Development of *Heterodera glycines* Ichinohe on soybean, *Glycine max* (L.) Merr. under gnotobiotic conditions. *J. Nematol.* 15, 272–281.
- Melton, T.A., Jacobsen, B.J., Noel, G.R., 1986. Effects of temperature on development of *Heterodera glycines* on *Glycine max* and *Phaseolus vulgaris*. *J. Nematol.* 18, 468–474.
- Mimee, B., Peng, H., Popovic, V., Duceppe, M.O., Tetreault, M.P., Belair, G., 2014. First report of soybean cyst nematode (*Heterodera glycines* Ichinohe) on soybean in the Province of Quebec. *Can. Plant Dis.* 98, 429.
- Mimee, B., Gagnon, A.-É., Colton-Gagnon, K., et Tremblay, É., 2016. Portrait de la situation du nématode à kyste du soja (*Heterodera glycines*) au Québec (2013–2015). *Phytoprotection* 96, 33–42.
- Nafziger, E., 2009. Soybean. Illinois Agronomy Handbook, 24th Edition. University of Illinois at Urbana-Champaign, College of Agriculture, Cooperative Extension Service, pp. 27–36.
- Nelson, B.D., Bradley, C.A., 2003. Soybean Cyst Nematode. Retrieved from. [Nov 2017]. <https://www.ndsu.edu/pubweb/~bernelso/soydisseases/cyst.shtml>.
- Newton, A.C., Torrance, L., Holden, N., Toth, I.K., Cooke, D.E., Blok, V., Gilroy, E.M., 2012. Climate change and defense against pathogens in plants. *Adv. Appl. Microbiol.* 81, 89–132.
- OMAFRA, 2009. Soybean - planting and crop development. In: Brown, C. (Ed.), Agronomy Guide for Field Crop. Service Ontario Publications, Toronto Retrieved from. <http://www.omafra.gov.on.ca/english/crops/pub811/pub811ch2.pdf> [Oct 2017].
- Orf, J., 2013. Breeding for SCN Resistance in the North. Presentation Conducted During Soybean Breeders' Workshop. Retrieved from. St. Louis, Missouri [Nov 2017]. [http://soybase.org/meeting\\_presentations/soybean\\_breeders\\_workshop/SBW\\_2013/presentations/13SBW\\_tues.Orf.pdf](http://soybase.org/meeting_presentations/soybean_breeders_workshop/SBW_2013/presentations/13SBW_tues.Orf.pdf).
- Osborne, T., Rose, G., Wheeler, T., 2012. Variation in the global-scale impacts of climate change on crop productivity due to climate model uncertainty and adaptation. *Agric. For. Meteorol.* 170, 183–194.
- Pederson, P., Kumudini, S., Board, J. & Conley, S. P. 2008. Soybean Growth and Development. In: Using Foliar Fungicides to Manage Soybean Rust (Eds. Dorrance, A. E., Draper, M. A. & Hershman, D. E.), pp. 41–47, Media Distribution Communications and Technology, The Ohio State University, Columbus, Ohio.
- Plouffe, D., Bourgeois, G., Beaudry, N., Chouinard, G., Choquette, D., 2014. CIPRA - Computer Centre for Agricultural Pest Forecasting: Crop Guide. Agriculture and Agri-Food Canada. Technical Bulletin A42-119/2013E-PDF. 136 p.
- Riggs, R. D. 2004. Hosts Range. In: Biology and Management of the Soybean Cyst Nematode (Eds. Riggs, R. D. & Wrather, J. A.), pp. 107–114, Robert D. Riggs and J. Allen Wrather Schmitt and associates of Marcelline, Marcelline, MO.
- Rincker, K., Cary, T., Diers, B.W., 2017. Impact of soybean cyst nematode resistance on soybean yield. *Crop Sci.* 57, 1–10.
- Robinson, A.P., Conley, S.P., Volenec, J.J., Santini, J.B., 2009. Analysis of high yielding, early-planted soybean in Indiana. *Agron. J.* 101, 131–139.
- Ross, J.P., 1964. Effect of soil temperature on development of *Heterodera glycines* in

- soybean roots. *Phytopathology* 54, 1228–1231.
- Savary, S., Ficke, A., Aubertot, J.-N., Hollier, C., 2012. Crop losses due to diseases and their implications for global food production losses and food security. *Food Secur.* 4, 519–537.
- Setiyono, T.D., Cassman, K.G., Specht, J.E., Dobermann, A., Weiss, A., Yang, H., De Bruin, J.L., 2010. Simulation of soybean growth and yield in near-optimal growth conditions. *Field Crops Res.* 119, 161–174.
- Strange, R.N., Scott, P.R., 2005. Plant disease: a threat to global food security. *Annu. Rev. Phytopathol.* 43, 83–116.
- Sundström, J.F., Albiñ, A., Boqvist, S., Ljungvall, K., Marstorp, H., Martiñ, C., et al., 2014. Future threats to agricultural food production posed by environmental degradation, climate change, and animal and plant diseases – a risk analysis in three economic and climate settings. *Food Secur.* 6, 201–215.
- Thiemeßl, J.M., Gobiet, A., Leuprecht, A., 2011. Empirical-statistical downscaling and error correction of daily precipitation from regional climate models. *Int. J. Climatol.* 31, 1530–1544.
- Todd, T.C., 1993. Soybean planting date and maturity effects on *Heterodera glycines* and *Macrophomina phaseolina* in Southeastern Kansas. *J. Nematol.* 25, 731–737.
- Todd, T.C., Pearson, C.A.S., Schwenk, F.W., 1987. Effect of *Heterodera glycines* on charcoal rot severity in soybean cultivars resistant and susceptible to soybean cyst nematode. *Ann. Appl. Nematol.* 1, 35–40.
- Tylka, G.L., Marett, C.C., 2014. Distribution of the soybean cyst nematode, *Heterodera glycines*, in the United States and Canada: 1954 to 2014. *Plant Health Progress* 15, 13–15.
- University of Illinois at Urbana-Champaign, 1991. RPD No. 501 - The Soybean Cyst Nematode Problem. Retrieved from. [Nov 2017]. <http://ipm.illinois.edu/diseases/series500/rpd501/>.
- Urbanski, J., Mogi, M., O'Donnell, D., DeCotiis, M., Toma, T., Armbruster, P., 2012. Rapid adaptive evolution of photoperiodic response during invasion and range expansion across a climatic gradient. *Am. Nat.* 179, 490–500.
- Iowa State University, 2004. Soybean Cyst Nematode. Integrated Crop Management, Iowa State University Extension and Outreach, Ames, Iowa. Retrieved from. [Nov 2017]. [http://crops.extension.iastate.edu/soybean/diseases\\_SCNbiology.html](http://crops.extension.iastate.edu/soybean/diseases_SCNbiology.html).
- Van Vuuren, D.P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, a., Hibbard, K., et al., 2011. The representative concentration pathways: an overview. *Clim. Change* 109, 5–31.
- Voldoire, A., Sanchez-Gomez, E., Salas y Mélia, D., Decharme, B., Cassou, C., Sénési, S., 2011. The CNRM-CM5.1 global climate model: description and basic evaluation. *Clim. Dyn.* 40, 2091–2121.
- Volodin, E.M., Dianskii, N.A., Gusev, A.V., 2010. Simulating present-day climate with the INMCM4.0 coupled model of the atmospheric and oceanic general circulations. *Atmos. Oceanic Phys.* 46, 414–431.
- Wang, J., Niblack, T.L., Tremain, J.A., Wiebold, W., Tylka, G.L., Marett, C.C., et al., 2003. Soybean cyst nematode reduces soybean yield without causing obvious aboveground symptoms. *Plant Dis.* 87, 623–628.
- Watanabe, M., Suzuki, T., Oishi, R., Komuro, Y., Watanabe, S., Emori, S., et al., 2010. Improved climate simulation by MIROC5: mean states, variability, and climate sensitivity. *J. Clim.* 23, 6312–6335.
- Wrather, J.A., Anand, S.C., 1988. Relationship between time of infection with *Heterodera glycines* and soybean yield. *J. Nematol.* 20 (3), 439–442.
- Wrather, J.A., Koenning, S.R., 2009. Effects of diseases on soybean yields in the United States 1996 to 2007. *Plant Health Prog.* 11, 1–8. <https://doi.org/10.1094/PHP-2009-0401-01-RS>.
- Wrather, J.A., Shannon, G., Balardin, R., Carregal, M., Escobar, R., Gupta, G.K., et al., 2010. Effect of diseases on soybean yield in the top eight producing countries in 2006. *Plant Health Prog.* <https://doi.org/10.1094/PHP-2010-0125-01-RS>.
- Yan, W., Hunt, L.A., 1999. An equation for modelling the temperature response of plants using only the cardinal temperatures. *Ann. Bot.* 84, 607–614.
- Zhang, L., Wang, R., Hesketh, J.D., 2000. Effects of photoperiod on growth and development of soybean floral bud in different maturity. *Agron. J.* 93, 944–948.
- Zhao, C., Liu, C., Piao, S., Wang, X., Lobell, D.B., Huang, Y., Asseng, S., 2017. Temperature increase reduces global yields of major crops in four independent estimates. *Proc. Natl. Acad. Sci. U. S. A.* 114 (35), 9326–9331.